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New Species and New Records of Podostemaceae from Phitsanulok Province, Northern Thailand

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Previous studies recorded two genera and three species of Podostemaceae from a single river in Phitsanulok Province, northern Thailand. Recent extensive field research resulted in finding six additional species, i.e., two new species (*Dalzellia sparsa* and *Hydrobryum mandaengense*) and four new records for the province (*Terniopsis minor, Thawatchaia trilobata, Hy. phetchabunense*, and *Hy. tardhuangense*). *Dalzellia sparsa* is characterized by the various leaves on the cupule, and *Hy. mandaengense* has disporangiate anthers with tortuous dehiscence. In total, five genera and nine species (five of which belong to *Hydrobryum*) occur in the province, with the result that Phitsanulok is the second most species-rich province, next to the adjacent Loei, for Thai Podostemaceae. Eight of the nine species known from the province are endemic to Thailand; *Hy. tardhuangense* occurs also in Laos. Among the endemics, *D. sparsa, Hy. bifoliatum, Hy. kaengsophense* and *Hy. mandaengense* are restricted to one or two river systems in Phitsanulok; the remaining four species occur widely. The descriptions of *Hanseniella heterophylla, Hy. phetchabunense*, and *Hy. tardhuangense* is emended using new collections. A key to all 49 species of Thailand has been updated.

Key words: *Dalzellia sparsa, Hanseniella, Hydrobryum mandaengense,* Phitsanulok, Podostemaceae, *Terniopsis,* Thailand, *Thawatchaia*

Podostemaceae comprise a unique aquatic family of submerged angiosperms in open, sunny habitats in torrential water of tropical and subtropical rivers in seasonal climates, and attached to rocks or boulders in waterfalls and river-rapids (Cook 1996, Cook & Rutishauser 2007). The plants emerge above the water to produce flowers and fruits only in the dry season (Willis 1902, Kato 2013). Wherever water levels are seasonally unchanged in natural or artificial conditions, the plants are incapable of completing their life cycle. Due to this special habitat, Podostemaceae have been poorly collected compared with terrestrial plants. Knowledge of their significance in flora has therefore been limited.

The family Podostemaceae comprises approximately 54 genera and 300 species in three subfamilies (Cook & Rutishauser 2007, Koi *et al.* 2012). Subfamily Podostemoideae, the most diverse (ca. 47 genera and ca. 280 species), is distributed worldwide, Tristichoideae (6 genera and ca. 19 species) is mainly distributed in Asia, with exception of *Tristicha trifaria* (Bory ex Willd.) Spreng., which is widely dispersed from Central and South America to Africa, and Weddellinoideae (a monotypic genus), which is confined to South America (Kato 2006a). The three subfamilies can be separated by floral features. Podostemoideae exhibits zygomorphic flowers with reduced tepals, young flowers enclosed in spathella, and shares bicarpellate pistils with Weddellinoideae; Tristichoideae has actinomorphic flowers with distinct tepals in common with Weddellinoideae, but its pistil is tricarpellate (Cook & Rutishauser 2007).

Thailand is the most species-rich area in Southeast Asia for Podostemaceae (Kato 2006a). The podostemads are distributed throughout the country in mountain streams associated with rushing currents. Ten genera and 47 species are recognized, a few of which are shared with Laos and other adjacent Asian countries (Cusset 1973a, b, 1992, Cusset & Cusset 1988, Kato & Kita 2003, Kato 2004, 2006b, 2008, 2011, 2013, Kato *et al*. 2004, Koi *et al*. 2008, Kato & Koi 2009, Koi & Kato 2012, 2015a, 2015b, Werukamkul *et al*. 2012; S. Koi & M. Kato unpubl. data). About two-thirds (27 spp.) of the species are endemic to Thailand. Loei Province in northeastern Thailand is a hot spot with the largest number of species (12) (Werukamkul *et al*. 2012). It is followed by Chiang Mai Province (8 spp.) in northern Thailand and Ubon Ratchathani Province (7 spp.) in eastern Thailand (Kato 2004, 2006b, Kato & Koi 2009).

Two genera and three species have been reported from Phitsanulok Province, two species (*Hanseniella heterophylla* C. Cusset, *Hydrobryum bifoliatum* C. Cusset) by Cusset (1992) and one species (*Hy. kaengsophense* M. Kato) by Kato (2004), all from the Kaeng Sopha waterfall, Tung Salaeng Luang National Park. These records are based on poor collections. Geographically, many waterfalls and rapids suitable for Podostemaceae are in the eastern part of Phitsanulok. Considering the high species diversity of Loei to the immediate east of Phitsanulok, the Podostemaceae of Phitsanulok are potentially more diverse than shown by previous studies. During the past four years, we have explored Phitsanulok extensively to document its flora and geographic distributions, and to estimate the conservation status of the plants there.

Based on recent collections, we report nine species, including two new species, four new records for Phitsanulok, and three endemic species for which numerous specimens were added. The descriptions are emended for three species, which were described based on a few specimens, since the recent collections exhibit greater variation than indicated in the protologues. A key to the species of Thailand is updated to help in understanding the diversity of Podostemaceae.

Materials and Methods

Phitsanulok Province (Fig. 1) occupies the southeastern part of northern Thailand with the Phetchabun Mountain Range near the border of Loei and Phetchabun Provinces. Phitsanulok, situated at 16°31'–17°44' N, 99°52'–101°04' E, covers an area of approximately 10,816 km^2. Climate in the region is tropical savannah, type *Aw* in Köppen climate classification, with low precipitation and distinct dry and wet seasons, usually differentiated into 3 seasons, i.e., the cool season from November to February, the hot season from March to mid May, and wet season from mid May to October. One third of the area, covering the eastern and northern parts of the province, is a mountain region ranging from 772 m to 2,102 m above sea level.

Field observations and collections were conducted in various waterfalls and rapids in Phitsanulok Province (Fig. 1). Specimens were fixed in FAA (formaldehyde : acetic acid : 50% ethyl alcohol = 5 : 5 : 90) and dried with silica gel for morphological and molecular analyses, respectively. The taxonomic recognition of species is based on comparative morphology and molecular phylogenetic analysis (Koi *et al*. 2012, P. Werukamkul & S. Koi unpubl. data). We measured quantitative characters based on 50 observed samples of organs (N = 50, rarely 100); otherwise the numbers of samples are indicated. Among the measured characters, the pedicel was measured from the node attached with cupule or spathella (special organs enclosing flower buds) to the node with a tepal; the gynophore was measured from the node with stamen to the base of the ovary. IUCN categories (IUCN Standards and Petitions Subcommittee 2014) were applied to each species.

All specimens examined were collected by Petcharat Werukamkul and La-aw Ampornpan, or Masahiro Kato, Satoshi Koi, P. Werukamkul, and L. Ampornpan. The collectors' names in the descriptions below are abbreviated as PW & LA or MK et al., respectively. The specimens are deposited in Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand (BKF); the Department of Biology, Srinakharinwirot University, Bangkok, Thailand; and the Herbarium of Department of Botany, National Museum of Nature and Science, Tsukuba, Japan (TNS).

Results and Discussion

Five genera and nine species of Podostemaceae are recorded from Phitsanulok Province. They include *Dalzellia sparsa*, sp. nov. (subfamily Tristichoideae) and *Hydrobryum mandaengense* sp. nov. (subfamily Podostemoideae). *Terniopsis minor* M. Kato & Koi, *Thawatchaia trilobata* M. Kato, Koi & Y. Kita, *Hy. tardhuangense* M. Kato and *Hy. phetchabunense* M. Kato & Koi are new records for the province. With nine species, Phitsanulok has the second largest number of species per province after Loei with 12 species (Werukamkul *et al*. 2012).

All species of *Hydrobryum* reported in the previous studies (e.g., Kato 2004, Kato & Koi 2009, Koi & Kato 2012, Werukamkul *et al*. 2012) show bithecal and tetrasporangiate anthers dehiscing longitudinally and introrsely, but *Hy. mandaengense* presents disporangiate anthers with one functional pollen sac per theca that opens tortuously lengthwise and introrsely (Fig. 3F). Such an anther has never been reported elsewhere in the family. The pollen grains are shed as monads in all Thai species of subfamily Tristichoideae and as dyads in those of the subfamily Podostemoideae.

Among the species in Phitsanulok, *Hydrobryum tardhuangense* also occurs in northern central Laos (Koi & Kato 2012); the remaining species are endemic to Thailand. *Hydrobryum kaengsophense*, *Hy. bifoliatum*, *Hy. mandaengense* and *Dalzellia sparsa* are restricted to Phitsanulok and present in one or two areas (Fig. 1). *Hanseniella heterophylla* is most abundant and dense in Khek River (including Kaeng Sopha waterfall) but forms small patches in the other three localities. Moreover, *Ha. heterophylla*, *Hy. bifoliatum* and *Hy. kaengsophense* are sympatric in Kaeng Sopha waterfall, where *Ha. heterophylla* occupies more than two thirds of area and grows on the upper part of rocks exposed earlier than the other two species. *Hydrobryum bifoliatum* and *Hy. kaengsophense* often grow intermixed on the same rock. *Dalzellia sparsa* is sympatric with *Hy. phetchabunense* in Kaeng Lad waterfall, where a population of *Dalzellia* is downstream of water flow and *Hy. phetchabunense* is scattered upstream. *Dalzellia sparsa* also is sympatric with *Hy. phetchabunense*, *Thawatchaia trilobata* and *Terniopsis minor* in Khlong Chompu stream (Fig. 1), where they are attached to flat rocks. Applying IUCN categories (2014), two species are estimated as Critically Endangered, three are Vulnerable, three are Near Threatened and one is Least Concern.

Including the present discoveries, Podostemaceae of Thailand comprise 10 genera (ca. 19% of the world's 54 genera) and 49 species (ca. 16% of the world's 300 species). They include seven genera and 35 species of subfamily Podostemoideae, and three genera and 14 species of Tristichoideae (Cusset 1992, Kato 2004, 2006b, Kato & Koi 2009, Werukamkul *et al*. 2012). *Hydrobryum* in Thailand is the largest within the genera of Podostemaceae in Thailand, and comprises 15 of the 27 species reported worldwide (including the new species and new species from Lao [Koi & Kato 2015b]) (Cusset 1992, Kato 2004, 2006b, 2008, Kato & Koi 2009, Koi & Kato 2012, Werukamkul *et al*. 2012).

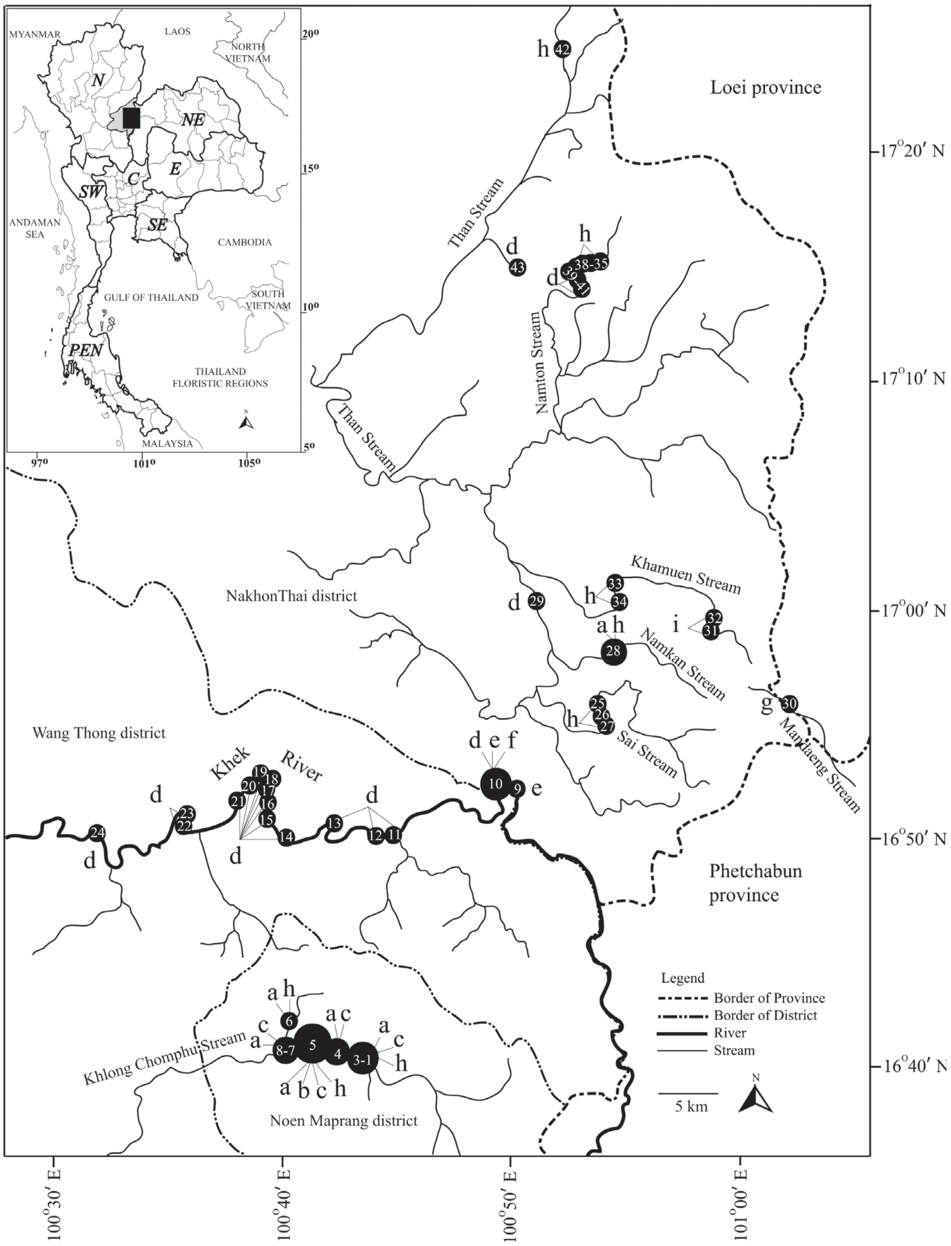

FIG. 1. Map of part of Phitsanulok Province, showing distribution of Podostemaceae. Area on main map corresponds to solid square in inset; hatched area indicates Phitsanulok Province. Letters (a–g) indicate species; solid circles indicate localities. Numbers (1–43) within solid circles indicate waterfalls/rapids and are consecutive with water flow. a, *Dalzellia sparsa*; b, *Terniopsis minor*; c, *Thawatchaia trilobata*; d, *Hanseniella heterophylla*; e, *Hydrobryum bifoliatum*; f, *Hy. kaengsophense*; g, *Hy. mandaengense*; h, *Hy. phetchabunense*; i, *Hy. tardhuangense*. 1 Kaeng Pak Khlong Khunkrajiak, 2 Kaeng Wang Tham Sang, 3 Kaeng Wang Kadum, 4 Kaeng Pak Kasao, 5 Kaeng Kanna, 6 Kaeng Wang Samnak, 7 Kaeng Taiwang-on, 8 Kaeng Wang Takiannoi, 9 Kaeng Hom, 10 Kaeng Sopha waterfall, 11 Poi waterfall, 12 Kaeng Pakhao Krayang, 13 Kaeng Kukla, 14 Kaeng S P Hut, 15 Kaeng Sai, 16 Kaeng Moradokpa, 17 Kaeng Hinlad, 18 Kaeng Ratchamung, 19 Kaeng Sang, 20 Kaeng Sopharam, 21 Kaeng Yao, 22 Kaeng Tinthai Bon, 23 Kaeng Tinthai Lang, 24 Sakunothayan waterfall, 25 Kaeng Pak Nao waterfall, 26 Kaeng Sapung waterfall, 27 Kaeng Hin Sai waterfall, 28 Kaeng Lad waterfall, 29 Kaeng Huataek, 30 Mandaeng waterfall, 31 Water Turbine, 32 Romklao Pharadon waterfall, 33 Pha Lad waterfall, 34 Kaeng Khamuen, 35 Pha Tairuea waterfall, 36 Wanglum Bon waterfall, 37 Wanglum Lang waterfall, 38 Tadyai waterfall, 39 Tadtinmee waterfall, 40 Tadtam waterfall, 41 Wanglum waterfall, 42 Huai Taleo waterfall, 43 Tintok waterfall.

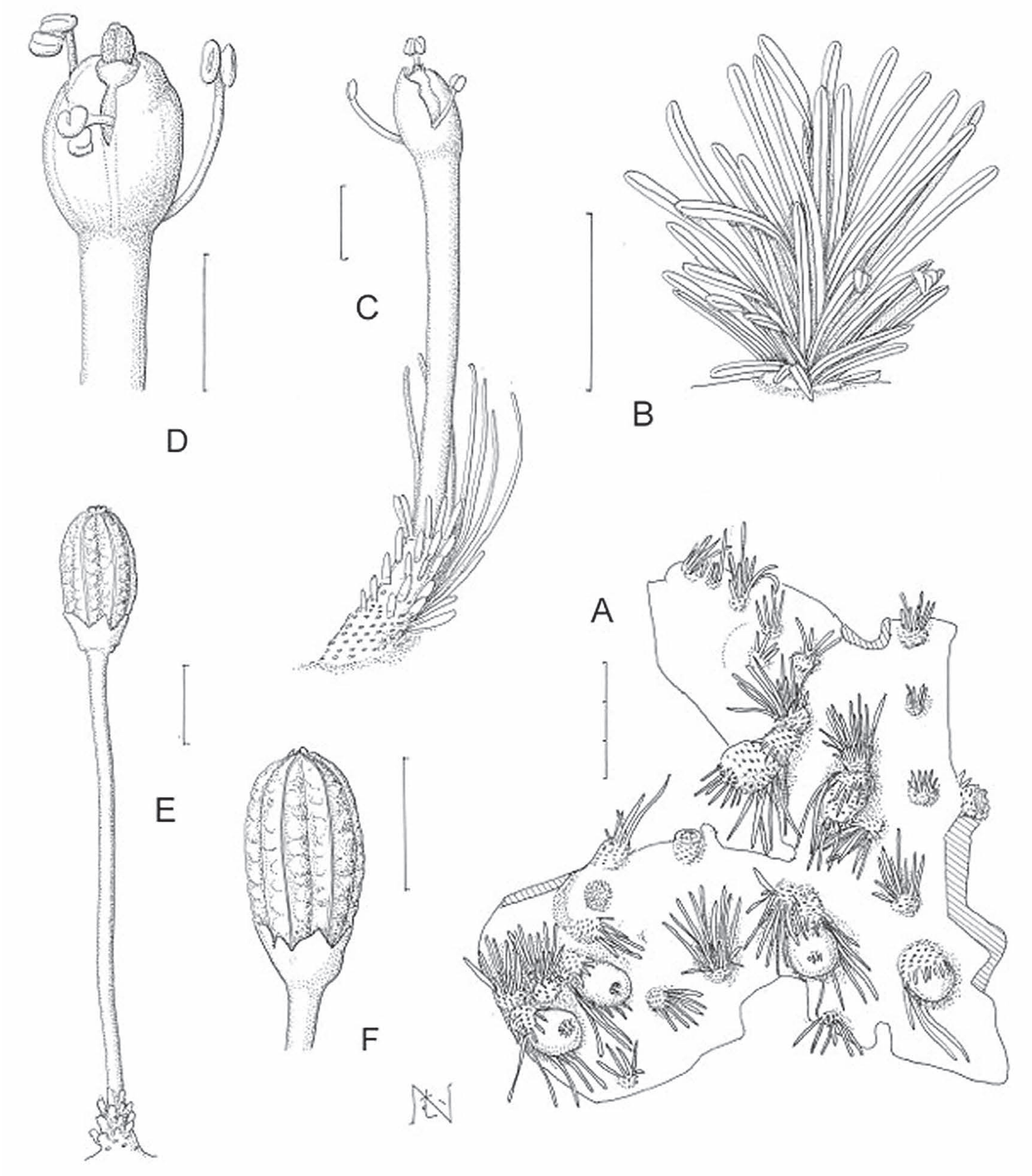

FIG. 2. *Dalzellia sparsa* (A, B, *TWA-175*; C, D, *TWA-216*; E, F, *TWA-204*). A. Crustose shoot with cupules and rosettes on dorsal surface. B. Rosette. C. Flower shoot extruded from cupule. D. Flower. E. Fruit. F. Capsule. Scale = 3 mm in A,2mm in B, 1 mm in C–F.

Taxonomic treatment

Subfamily Tristichoideae

1. Dalzellia sparsa Ampornpan, Werukamkul, M. Kato & Koi, **sp. nov**. —Fig. 2.

Differs from congeners in the longer leaves of the rosette (to ca. 6 mm *vs*. 3 mm in other congeners) and leaves on the cupule variably distributed, i.e., persistent and short on the distal mouth, sparse or subglabrous in the middle zone, dense and long at the base (to ca. 5 mm *vs*. to 2(-5) mm).

Typus. Phitsanulok Province: Thailand. Nakhon Thai

District, Kaeng Lad waterfall, 312 m alt., 16°57'09.1″ N, 100°55'07.0″ E, 10 Dec. 2011, st. fl. fr., *P. Werukamkul & L. Ampornpan TWA-216* (holotype BKF; isotype TNS).

Herbs, rheophilous, annual, roots absent. Shoot attached to rock surface by adhesive hairs on ventral surface, 0.3–0.7 (median, 0.5) mm thick, isotomously and anisotomously lobed; lobes radiating from center, broadly ribbon-like, 1.5–5(–9) (2) mm wide. Leaves dimorphic, univeined, borne on upper surface in longitudinal rows; dorsal leaves caducous, linear, apex obtuse, 0.5–2.6 (1.5) mm long, 0.1–0.3 (0.2) mm wide, leaves close to edge of shoot gradually longer and transitioning to cupule leaves; leaves of rosette (rosettes borne on older part of shoot), linear, 0.5-6.2 (2.6) mm long, 0.1–0.3 (0.1) mm wide, fimbriate, apex obtuse; outer leaves shorter; marginal leaves fimbriate, lanceolate, 1–4 (2.5) mm long, 0.3–0.6 (0.5) mm wide at base, apex obtuse. Flower bud enclosed by leafy cupule on lobe margin, cupules 1.5–3 (1.9) mm long, 1–1.6 (1.2) mm thick; leaves on cupule variably distributed, persistent and short at distal mouth, sparse or subglabrous and caducous in middle zone, dense in basal zone; basal leaves on ventral surface (facing shoot) lanceolate, 0.5–5 (2) mm long, 0.05–1 (0.2) mm wide, leaves on dorsal surface linear, 0.5–4.1 (1) mm long, 0.05–0.3 (0.1) mm wide; pedicel 1.5–10 (3.5) mm long at anthesis; tepals 3, membranaceous, 1.2–2.3 (2) mm long, as long as ovary, 3-lobed, lobes hemi-ovate, 1/3–1/2 deep from apex or 0.3–1 (0.6) mm; stamens 3, free, alternate to tepals, 1.5–3.5 (2.5) mm long including anthers, longer than pistil; anthers globose-ovoid, basifixed, bilobed, tetrasporangiate, dehiscing introrsely and longitudinally, 0.3–0.5 (0.5) mm long, 0.3–0.5 (0.4) mm wide, pollen in monads; ovary obovoid-ellipsoid, 1–2 (1.7) mm long, 0.5–1 (0.9) mm wide, 3-locular; stigmas 3, free, 0.2–0.5 (0.4) mm long, subdeltate, triangle, densely papillate, papillae elongate; ovules 20–54 (34) per locule, placentation axile; capsules stalked (stalk 2.5–10.3 (5) mm long), trigonous, obovoid, 1.5–2 (1.8) mm long, 0.7–1.1 (0.9) mm wide, 9-ribbed, dehiscing by 3 valves; seeds 40–124 (82) per capsule, dried seeds 0.18–0.34 (0.24) mm long, 0.08-0.17 (0.12) mm wide.

Distribution. Endemic to Phitsanulok Province, northern Thailand. *Dalzellia sparsa* was collected from two areas (Fig. 1). The population in Kaeng Lad waterfall is small, occupying an area estimated at 20 m^2. It is in serious danger of loss, estimated 60% decline, due to disturbances by recreational activities and agricultural effluents. It is thriving and healthy and forms dense mats in a series of rapids along Khlong Chompu stream (Fig. 1) in a mixed deciduous forest in Tung Salaeng Luang National Park. The extent of occurrence and area of occupancy are estimated at 163 km^2 and 3,447 m^2, respectively.

Conservation status. Vulnerable (VU D2)

Other specimens examined. Northern Thailand, Phitsanulok Prov.: Nakhon Thai Dist., Kaeng Lad waterfall, 312 m alt., 16°57'09.1″ N, 100°55'07.0″ E, 19 Dec. 2010, st. fl. fr., *PW & LA TWA-175*; 29 Jan. 2011, fl. fr., *PW & LA TWA-204*; 5 Dec. 2012, st. fl., *PW & LA TWA-225*; 23 Feb. 2015, fr., *MK et al. TL-1910*. Noen Maprang Dist., Tung Salaeng Luang National Park, Khlong Chompu stream, Kaeng Kanna, 81 m alt., 16°41'12.8″ N, 100°43'07.6″ E, 9 Feb. 2014, st. fl. fr., *PW & LA TWA-266*; 8 Apr. 2014, fr., *PW & LA TWA-292*; Kaeng Pak Kasao, 81 m alt., 16°41'11.2″ N, 100°43'22.7″ E, 9 Feb. 2014, st. fl. fr., *PW & LA TWA-270*; Kaeng Wang Kadum, 96 m alt., 16°40'37.3″ N, 100°43'32.1″ E, 10 Feb. 2014, st. fl. fr., *PW & LA TWA-272*; Kaeng Wang Tham Sang, 96 m alt., 16°40'47.0″ N, 100°43'36.8″ E, 10 Feb. 2014, st. fl. fr., *PW & LA TWA-276*; Kaeng Pak Khlong Khunkrajiak, 97 m alt., 16°40'22.1″ N, 100°43'48.1″ E, 10 Feb. 2014, st. fl. fr., *PW & LA TWA-279*; Kaeng Wang Samnak, 104 m alt., 16°43'23.9″ N, 100°41'18.2″ E, 8 Apr. 2014, fr., *PW & LA TWA-294*; Kaeng Taiwang-on, 77 m alt., 16°41'10.6″ N, 100°42'55.3″ E, 8 Apr. 2014, fr., *PW & LA TWA-296*; Kaeng Wang Takiannoi, 80 m alt., 16°41'07.9″ N, 100°42'44.8″ E, 8 Apr. 2014, fr., *PW & LA TWA-298*.

Notes. All the species of southeast Asian *Dalzellia* form a monophyletic sister group of the Indo-Sri Lankan *D. zeylanica* (Gardner) Wight, sensu lato (Koi *et al*. 2012). *Dalzellia sparsa* is distinguished from other Thai congeners in having longer rosette leaves (to ca. 6 mm *vs*. 3 mm in others) and in the variable distribution of leaves on the cupule, i.e., persistent and short on the distal mouth, sparse or subglabrous in the middle, dense and long at the base (to ca. 5 mm *vs*. to 2(–5) mm). *Dalzellia sparsa* is similar to *D. angustissima* M. Kato in the globose-ovoid anthers (*vs.* subglobose in *D. angustissima*) and in having 20–54 ovules per locule (*vs.* 30–50 in *D. angustissima*), and to the other Thai *Dalzellia* in the length of the pedicel (1.5–10 *vs.* 2–8 mm in other species of *Dalzellia* in Thailand, except *D. kailarsenii* M. Kato which has the shortest at 1.5–2 mm). The width of shoot lobes is moderate (1.5–5 mm) compared with the broad shoots of *D. ubonensis* M. Kato (3–20 mm) and *D. ranongensis* M. Kato (3–10 mm), and the narrow shoots of *D. kailarsenii* (1.5–2.5 mm) and *D. angustissima* (1–1.5 mm).

2. Terniopsis minor M. Kato & Koi in Gard. Bull. Singapore 61(1): 75–58, f. 2. 2009.

Distribution. Endemic to Thailand. Previously known in southeastern (Trat and Chanthaburi) and central (Nakhon Nayok) Thailand (Kato & Koi 2009). In the present study, it was found in a single rapid of a series of rapids, forming an unhealthy colony in Khlong Chompu stream in Phitsanulok Province (Fig. 1), northern Thailand. The total extent of occurrence is estimated at 11,088 km^2.

Conservation status. Vulnerable [VU B1ab(ii, iii)]

Specimens examined. Northern Thailand, Phitsanulok Prov.: Noen Maprang Dist., Tung Salaeng Luang Natl. Park, Klong Chompu Stream, Kaeng Kanna, 81 m alt., 16°41'12.8″ N, 100°43'07.6″ E, 9 Feb. 2014, st. buds, *PW & LA TWA-269*; 8 Apr. 2014, decomposed st., fl., fr., *PW & LA TWA-290*.

Notes. The specimens from Phitsanulok differ from specimens from Chanthaburi, Nakon Nayok and Trat by having more ramuli in association with the flowering shoot (1–4 *vs.* one ramulus) and the variable number of ovules per locule (13–24 *vs.* ca. 20).

Subfamily Podostemoideae

3. Hanseniella heterophylla C. Cusset in Bull. Mus. Natl. Hist. Nat. Paris, 4^e Sect. B, Adansonia 14(1): 36, f. 6. 1992; Kato in Acta Phytotax. Geobot. 55(3): 139, f. 2. 2004.

Herbs, rheophilous, annual. Root crustaceous, tightly attached to rocks by adhesive hairs on lower surface, irregularly lobed, dark green, 0.1–0.5 (median, 0.3) mm thick, lobes 5–24 (12) mm wide; leaves tufted, scattered on dorsal surface of root, 2–7 (5) per tuft, linear, needle-like, 1–4 (1.6) mm long. Flowering shoots scattered on dorsal surface of root, 2.5–6 (3.5) mm long, 1.7–3 (2.5) mm wide, erect or slightly oblique; bracts green or crimson red, thick, imbricate, in 4 rows (2 ventral and 2 dorsal), 3–6 (5) per row, upper bracts gradually larger, dimorphic, bracts in adjacent rows occasionally connate; ventral bracts (facing root) obovate, oblong 1–4 (2) mm long, 0.7–2 (1) mm wide, 2-lobed (occasionally 3-lobed) 1/2 to base, lobes 0.6–1.8 (1.1) mm deep, apex obtuse or bluntly rounded or lower one acute; dorsal bracts entire, abaxially carinate; uppermost bracts bilaterally asymmetric, deltate, rectangular, 1–3 (2) mm long, 0.4–1.2 (0.8) mm wide, apex subtruncate or round; lower bracts symmetric, subacute; spathella enclosing flower bud, ellipsoid, thick, 0.3–1.2 (1) mm long, apical portion with 3 thick ridges, rupturing transversely at base of ridges on dorsal surface; flower terminal, solitary; pedicel 0.5–2 (1) mm long; tepals 2, one on each side of andropodium, scale-like, linear, 2.2–4.5 (3) mm long, apex acute; stamens 2, rarely 3, 4.3–8 (6.1) mm long including anthers, exceeding pistil, branched near middle, andropodium 2–5.5 (3.5) mm long, as long as ovary or lower to middle part of ovary, andropodium and filament flattened; anthers quadrangular, theca equal, red when fresh, basifixed, tetrasporangiate, dehiscing introrsely and longitudinally, 0.6–1.4 (1) mm long, 0.5–1 (0.7) mm wide, pollen in dyads; gynophore 0.7–4 (2) mm long; ovary 1, 2-locular, ellipsoid, slightly flattened, 1.5–2.7 (2.5) mm long, 0.7–1.3 (1) mm wide; stigmas bifid, upright prior to spathella rupture, forked near base, needle-like, pointed, equal or subequal, 0.4–1.5 (0.8) mm long, fused stigma, 0.1–0.2 (0.1) mm long; ovules 0.36–0.84 (0.65) mm long, 0.24–0.5 (0.36) mm wide, 4–8 (5) per locule, borne on placental margin interrupted by sterile middle part or with additional ovule in upper central portion; stalk of capsule 2–8 (4) mm long; capsule ellipsoid, slightly flattened, 1.1–2.5 (2.3) mm long, 0.8–1.1 (1) mm wide, 8–16 (12)-ribbed including shorter and thinner ribs, dehiscing by two equal valves, valves persistent, seeds 2-16 (10) per capsule, dried seeds 0.46–0.96 (0.7) mm long, 0.24–0.58 (0.36) mm wide.

Distribution. Endemic to northern (Phitsanulok) and northeastern [Loei (Kato 2004, Werukamkul *et al*. 2012)] Thailand. *Hanseniella heterophylla* occurs in four rivers and streams in Phitsanulok (Fig. 1) and two rivers in Loei (Kato 2004, Werukamkul *et al*. 2012). Due to disturbances and pollutants, decline is estimated at 20% at Kaeng Sopha waterfall and 50% at Kaeng Huataek in Sai stream. The area of occupancy at Kaeng Huataek is estimated to be only 20 m^2. The major population occurs in Khek River (Fig. 1) where the plants form dense growth on rock outcrops in a series of rapids along Khek River where whitewater rafting activities takes place annually. The rafting activities during high water during the rainy season apparently have no impact on the growth of the plants. The other two locations (Namton and Than streams) are in the forest in Phu Kad Wildlife Sanctuary. The extent of occurrence and area of occupancy is estimated at 2,291 km^2 and 10,499 m^2, respectively.

Conservation status. Near Threatened (NT).

Specimens examined. Northern Thailand, Phitsanulok Prov.: Nakhon Thai Dist., Tung Salaeng Luang Natl. Park, Khek River, Kaeng Sopha waterfall, 408 m alt., 16°52'17.6″ N, 100°50'05.7″ E, 4 Dec. 2010, st. fl. fr., *PW & LA TWA-160/1*; 10 Dec. 2011, fl. fr., *PW & LA TWA-212, TWA-213*. Wang Thong Dist., Khek River, Sakunothayan Waterfall Arboretum, 25 m alt., 16°50'14.3″ N, 100°31'48.4″ E, 5 Dec. 2010, fl., *PW & LA TWA-160/2*; Kaeng Tin Thai Bon 62 m alt., 16°51'07.1″ N, 100°36'28.8″ E, 5 Dec. 2010, fl. fr., *PW & LA TWA-161*; Poi waterfall, 198 m alt., 16°50'41.4″ N, 100°45'31.2″ E, 5 Dec. 2010, buds fl. fr., *PW & LA TWA-162*; 8 Dec. 2012, buds fl. fr., *PW & LA TWA-243*; 18 Jan. 2013, st. fl. fr., *PW & LA TWA-250*; Kaeng Moradokpa, 141 m alt., 16°52'26.8″ N, 100°39'49.0″ E, 7 Dec. 2012, fl. fr., *PW & LA TWA-236*; Kaeng Hinlad, 128 m alt., 16°52'42.3″ N, 100°39'21.4″ E, 7 Dec. 2012, fl. fr., *PW & LA TWA-237*; Kaeng Ratchamoung, 130 m alt., 16°53'10.7″ N, 100°39'24.6″ E, 7 Dec. 2012, fl. fr., *PW & LA TWA-238*; Kaeng Sang, 122 m alt., 16°53'11.9″ N, 100°39'05.8″ E, 7 Dec. 2012, fl. fr., *PW & LA TWA-239*; Kaeng Sopharam, 119 m alt., 16°53'04.3″ N, 100°38'55.4″ E, 7 Dec. 2012, fl. fr., *PW & LA TWA-240*; Kaeng Yao, 111 m alt., 16°52'49.7″ N, 100°38'26.1″ E, 7 Dec. 2012, fl. fr., *PW & LA TWA-241*; Kaeng Sai, 147 m alt., 16°51'34.9″ N, 100°39'47.5″ E, 7 Dec. 2012, fl. fr., *PW & LA TWA-242*; Kaeng Tin Thai Lang 88 m alt., 16°51'11.4″ N, 100°36'36.5″ E, 8 Dec. 2012, fl., *PW & LA TWA-246*; Kaeng S P Hut, 150 m alt., 16°50'38.5″ N, 100°40'41.2″ E, 18 Jan. 2013, fl. fr., *PW & LA TWA-248*; Kaeng Kukla, 172 m alt., 16°51'20.4″ N, 100°43'18.7″ E, 18 Jan. 2013, st. fl. fr., *PW & LA TWA-249*; Kaeng Pa-khao Krayang, 181 m alt., 16°50'28.5″ N, 100°44'27.4″ E, 18 Jan. 2013, st. fl. fr., *PW & LA TWA-251*. Nakhon Thai Dist.: Kaeng Huataek, 227 m alt., 17°03'45.0″ N, 100°51'59.8″ E, 9 Dec. 2011, buds fl. fr., *PW & LA TWA-211*; 5 Dec. 2012, buds fl. fr., *PW & LA TWA-227*; 18 Jan. 2013, buds fl. fr., *PW & LA TWA-247*; Phu Kad Wildlife Sanctuary, Tadtam waterfall, 271 m alt., 17°14'51.7″ N, 100°53'38.1″ E, 6 Dec. 2012, st., *PW & LA TWA-228*; 19 Jan. 2013, st., *PW & LA TWA-258*; Tadtinmee waterfall, 273 m alt., 17°14'53.9″ N, 100°53'47.6″ E, 6 Dec. 2012, st., *PW & LA TWA-229*; 19 Jan. 2013, st., *PW & LA TWA-257*; Wanglum waterfall, 293 m alt., 17°14'50.7″ N, 100°53'41.5″ E, 6 Dec. 2012, st., *PW & LA TWA-231*; 19 Jan. 2013, st., P*W & LA TWA-256*; Tintok waterfall, 228 m alt., 17°15'19.1″ N, 100°51'08.8″ E, 19 Jan. 2013, fl. fr., *PW & LA TWA-260*.

Notes. The above description is based on numerous specimens collected on recent explorations, compared with three specimens from two localities in Phitsanulok and Loei examined by Cusset (1992) and Kato (2004). The number of ribs on the capsule is variable. Individuals from the rapids and waterfalls in Khek River (Fig. 1), except *TWA-162* and *TWA-243*, have 12–16 (median, 12) ribs, including shorter and thinner ribs between the thicker ones. The number of ribs on the capsule is similar to that given in the description by Kato (2004). *TWA-162* and *TWA-243* from Poi waterfall in Khek River, along with the isolated population *TWA-211* from Kaeng Huataek, have 8–10 ribs; *TWA-260* from waterfalls in Phu Kad Wildlife Sanctuary has 8–12 ribs. A phylogenetic analysis (S. Koi unpubl. data) does not support distinguishing species by the number of ribs.

Hanseniella smitinandii M. Kato, the other species of the genus, is characterized by the up to 7(–8) bracts per row, the capsules 1–2 mm long and 0.4–0.7 mm thick, and the 8 ribs on the capsule, based on a single specimen collected in Fang, Chiang Mai, northern Thailand (Kato 2004). This study shows that the number of ribs in *Ha. heterophylla* is variable and ranges from 8 to 16, indicating that this character cannot separate the two species clearly. However, the species are separable by the number of bracts and the thickness of the capsule. Whether the two are independent species, varieties, or the same taxon requires further study of additional individuals from Chiang Mai.

4. Hydrobryum bifoliatum C. Cusset in Bull. Mus. Natl. Hist. Nat. Paris, 4^e Sect. B, Adansonia 14(1): 48, f. 10. 1992; Kato in Acta Phytotax. Geobot. 55(3): 145, f. 5. 2004.

Distribution. Endemic to Phitsanulok Province. Our extensive explorations found this species only in two neighboring areas in a single river (Fig. 1, e). It is sympatric with *Hanseniella heterophylla* and *Hydrobryum kaengsophense* in one of the two localities, Kaeng Sopha waterfall. The populations have declined by ca. 20% between 2010 and 2012 due to human impact and their narrow distribution. The extent of occurrence and area of occupancy are estimated at 13 km^2 and 35 m^2, respectively.

Conservation status. Critically Endangered [CR B1ab(ii, iii)+2ab(ii, iii)].

Noteworthy characters. Flowering shoots appressed and radiating from the center of the root; the bracts with large, sheath-like base, subtending the entire length of the ovary; the spathella ruptured apically, persistent and enclosing the ovary and capsule; bracts, spathellas, ovaries pink, and filaments whitish pink when fresh.

Specimens examined. Northern Thailand, Phitsanulok Prov.: Nakhon Thai Dist., Tung Salaeng Luang National Park, Kaeng Sopha waterfall, 408 m alt., 16°52'17.6″ N, 100°50'05.7″ E, 4 Dec. 2010, st. buds fl. fr., *PW & LA TWA-159*; 19 Dec. 2010, buds fl. fr., *PW & LA TWA-188*; 10 Dec. 2011, buds fl. fr., *PW & LA TWA-214/1*; 8 Dec. 2012, st. buds fl., *PW & LA TWA-245*; Kaeng Hom, 430 m alt., 16°52'35.4″ N, 100°50'25.5″ E, 10 Dec. 2011, st. buds fl. fr., *PW & LA TWA-217*; 8 Dec. 2012, st. buds fl. fr., *PW & LA TWA-244*.

5. Hydrobryum kaengsophense M. Kato in Acta Phytotax. Geobot. 55(3): 145, f. 6. 2004.

Distribution. Known only from the type locality (Kaeng Sopha waterfall, Tung Salaeng Luang National Park, Phitsanulok) in a very small distribution range (1,500m^2); the population is declining there. This distribution data is a result of our extensive explorations in this and neighboring provinces.

Conservation status. Critically Endangered [CR B1ab(ii, iii)+2ab(ii, iii)].

Specimens examined. Northern Thailand, Phitsanulok Prov.: Nakhon Thai Dist., Tung Salaeng Luang Natl. Park, Kaeng Sopha waterfall, 408 m alt., 16°52'17.6″ N, 100°50'05.7″ E, 4 Dec. 2010, st. buds fl. fr., *PW & LA TWA-159/2*; 10 Dec. 2011, buds fl. fr., *PW & LA TWA-214/2*; 8 Dec. 2012, st. buds fl. fr., *PW & LA TWA-245/2*.

Notes. Although all specimens were collected from the type locality, the following characters of the specimens collected for the present study show greater quantitative variation than indicated in the protologue: ovules 16-32 per locule (*vs*. 16-18 in Kato 2004); number of ribs 18-22 per capsule (*vs*. 12-14). Despite such large variation in morphology, a plant with many ovules and many capsular ribs (*TWA-245/2*) hardly differs from the type (*TL-312*) in the *matK* sequences (S. Koi unpubl. data). By contrast, the range of variation in other congeners is relatively small, even though, generally, an increase in the number of specimens makes variation greater (Werukamkul *et al.* 2012, Koi & Kato 2012).

6. Hydrobryum mandaengense

Ampornpan, Werukamkul, M. Kato & Koi, **sp. nov.** —Fig. 3.

Distinct from the congeners in the single stamen with disporangiate anther (one pollen sac per theca) that dehisces tortuously lengthwise and introrsely.

Typus. Phitsanulok Province: Thailand. Nakhon Thai District, Mandaeng waterfall, Phu Hin Rong Kla National Park, 1,172 m alt., 16°56'53″ N, 101°03'37.1″ E, 19 Dec. 2010, *P. Werukamkul & L. Ampornpan TWA-198* (holotype BKF; isotype TNS).

Herbs, rheophilous, annual. Roots green, crustaceous, tightly attached to rocks by adhesive hairs on lower surface, 0.06–0.24 (median, 0.12) mm thick, irregularly lobed, lobes 1–6 (2.1) mm wide; leaves tufted, scattered on dorsal surface of root, 1–4 (4) per tuft, surrounded by slightly raised fringe of root tissue, linear, gradually wider in upper portion, 0.5–3.5 (1.6) mm long, 0.1–0.3 (0.2) mm wide, apex acute or obtuse. Flowering shoots appressed, scattered on dorsal surface of root, 1.5–2.5 (2) mm long, 0.5–1.1 (0.9) mm wide; bracts 3–12 (6), in 2 rows, imbricate, papillate, 0.6–8 (4.5) mm long; base sheathing, deltate, 0.5–2 (1.1) mm long, 0.4–1.5 (0.9) mm wide, distal part caudate, acuminate or acute, 0.1–6 (3.4) mm long; spathella enclosing flower bud, papillate, rupturing longitudinally at anthesis; flower 1, terminal; pedicel 0.5–1.1 (0.7) mm long; tepals 2 on either side of stamen, linear, apex obtuse; stamen single, 2–4 (3) mm long including anther, as long as or slightly longer than pistil, filament 0.2–0.3 (0.3) mm wide; anther basifixed, deltoid, 0.3–0.6 (0.4) mm long, 0.4–0.7 (0.6) mm wide at base, base sagittate, apex retuse, theca ellipsoid, equal or slightly unequal, disporangiate (one pollen sac per theca), dehiscing obliquely longitudinally and tortuously, pollen in dyads; gynophore 0.5–1 (0.7) mm long; ovary 1, 2-locular, ellipsoid, flattened, 1.3–2 (1.6) mm long, 0.6–1 (0.9) mm wide; stigmas bifid, forked near base, 0.4–1 (0.5) mm long, linear, papillate, ventral stigma thicker than dorsal, equal or subequal; ovules 10–25 (16) per locule, borne on mostly the whole surface of placenta or except in central lower area, placentation axile; capsule stalks 1–2.1 (1.5) mm long; capsules ellipsoid, slightly flattened, 1.5–2.5 (2) mm long, 0.6–1.2 (1) mm wide, constantly 12-ribbed, dehiscing by two equal valves, valves persistent; seeds 10–38 (23) per capsule, flattened, elliptic ovate, 0.18–0.28 (0.25) mm long, 0.1–0.18 (0.13) mm wide.

Distribution. Endemic to Phitsanulok Province, northern Thailand. *Hydrobryum mandaengense* is known only from the type locality. The extent of occurrence and area of occupancy are estimated to be 5,000 m^2 and 150 m^2, respectively.

Conservation status. Vulnerable (UV D2).

Other specimen examined. Northern Thailand, Phitsanulok Prov.: Nakhon Thai Dist., Mandaeng waterfall, Phu Hin Rong Kla Natl. Park, 1,172 m alt., 16°56'53″ N, 101°03'37.1″ E, 4 Dec. 2010, st. buds fl. fr., *PW & LA TWA-158*; 24 Feb. 2015, fr., *MK et al. TL-1913*.

Notes. Although *Hydrobryum mandaengense* is not closely related to *Hy. khaoyaiense* M. Kato, they are most similar to each other. Both share the single stamen, to 4-mm long, and 2-locular ovaries. But *Hy. mandaengense* is different from *Hy. khaoyaiense* in the bracts with acute, acuminate or caudate tips (*vs*. obtuse), ovules borne mostly on the whole placental surface (*vs*. on margin), tepals never extending beyond mid-ovary (*vs*. higher than mid-ovary), and the constantly 12 ribs on the capsule (*vs*. 12–14 ribs). Phylogenetically, *Hy. mandaengense* is closely related to *Hy. tardhuangense* (P. Werukamkul & S. Koi unpubl. data) and shares with it the tufts of leaves surrounded by raised fringes of root tissue, the papillate, deltate bracts with an acute, acuminate or caudate apex, the papillate spathella, and the subequal stigmas. But it differs in its single stamen (*vs*. 2 stamens with common andropodium in *Hy. tardhuangense*).

7. Hydrobryum phetchabunense M. Kato & Koi in Gard. Bull. Singapore 61(1): 65, f. 6. 2009.

Herbs, rheophilous, annual. Roots crustaceous, tightly attached to rocks by adhesive hairs on the lower surface, green, irregularly lobed, 0.2–0.8 (median, 0.4) mm thick, lobes 5–27 (14)

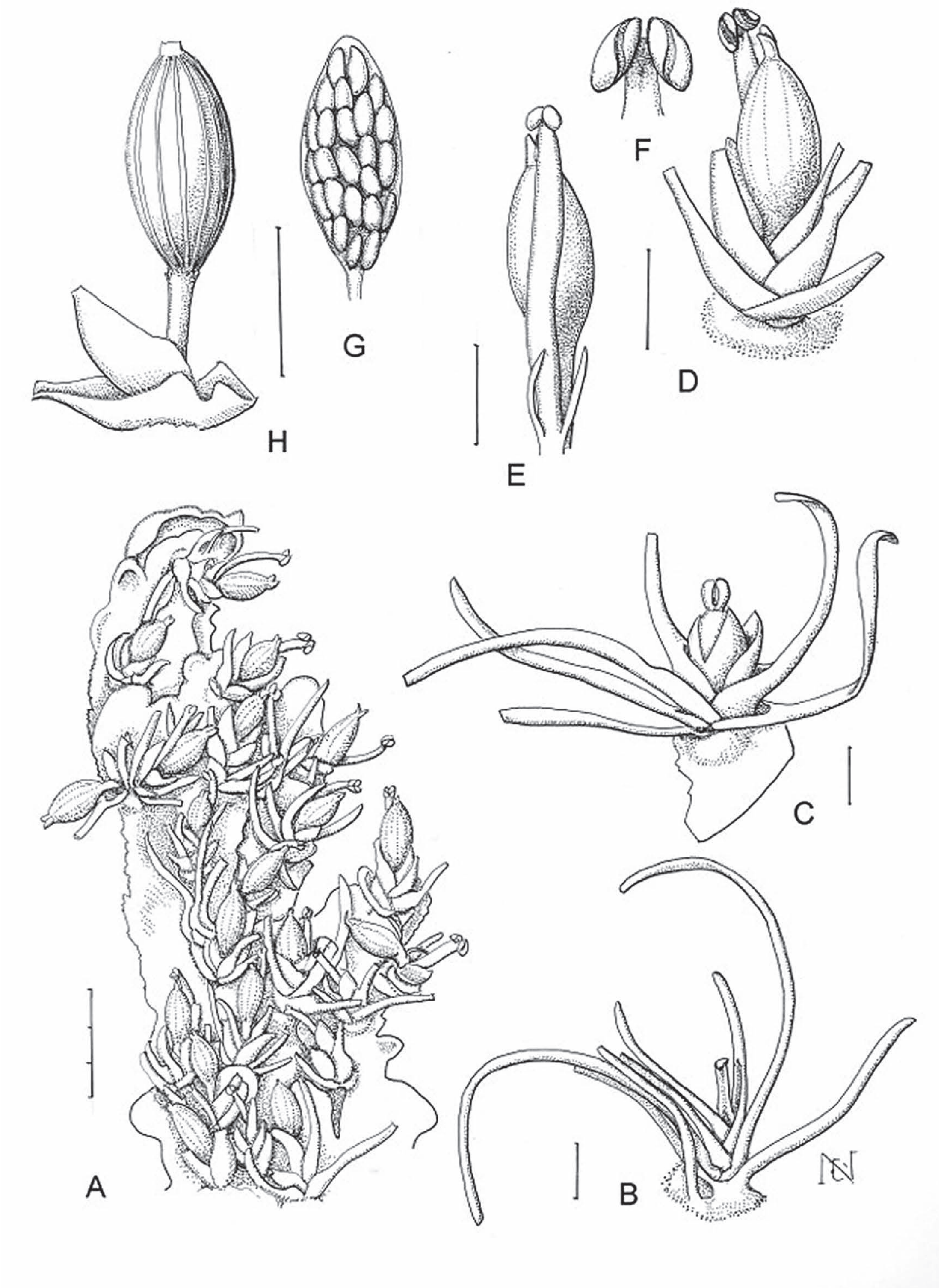

FIG. 3. *Hydrobryum mandaengense* (*TWA-198*). A. Crustose root with flowers on dorsal surface. B. Tuft of leaves. C. Flower bud subtended by bracts. Spathella is ruptured. D. Dorsal view of flower. E. Ventral view of flower. F. Anthers. G. Ovules on placenta surface. H. Fruit. Scale = 3 mm in A, 1 mm in B–E and G–H, 0.5 mm for F (bar for D).

mm wide; leaves tufted, scattered on dorsal surface of root, 1–4 (2) per tuft, surrounded by slightly raised fringe of root tissue, 1–6 (2) mm long, clavate, apex acute. Flowering shoots scattered on dorsal surface of root, appressed, oblique, 1.5–4 (2.5) mm long, 0.9–3 (2) mm wide; bracts 2–10 (4), in 2 rows, imbricate, distinctly papillate, triangular, ovate, 0.4–2.5 (1) mm long, 0.2–1.7 (0.8) mm wide, entire, apex obtuse; spathella enclosing flower bud, distinctly papillate, apex retuse, rupturing irregularly at anthesis, persistent; flower 1, terminal; pedicel 0.5–2.5 (1) mm long; tepals 2 on either side of andropodium, linear, 1.5–4 (2.5) mm long, variable in length, from longer to shorter than ovary, apex acute; stamens 2, 2.5–8.5 (5.5) mm long, longer than pistil, forked below middle, andropodium 0.5–5 (2.5) mm long, variable in length from shorter than mid ovary to longer than ovary, filaments patent; anthers basifixed, bilobed, thecae unequal, tetrasporangiate, quadrangular, 0.3–1 (0.7) mm long, 0.4–1 (0.7) mm wide, base obtuse, apex truncate, dehiscing introrsely and longitudinally, pollen in dyads; gynophore 0.5–3 (1.5) mm long; ovary 1, green, 2-locular, ellipsoid, flattened, 1–2.5 (2) mm long, 0.7–1.5 (1) mm wide; stigmas bifid, 0.3–1.5 (0.6) mm long, linear, pointed, curved, equal or subequal; ovules 5–23 (11) per locule, borne on placental margin, occasionally with 1–6 ovules on upper central area, placentation axile; capsule stalk 1–6 (2.5) mm long; capsule ellipsoid, flattened, 1–3 (2) mm long, 0.9–1.5 (1.1) mm wide, 14–18 (18)-ribbed, dehiscing by two equal valves, valves persistent; seeds 4–38 (15) per capsule, 0.3–0.72 (0.42) mm long, 0.14–0.38 (0.24) mm wide.

Distribution. Restricted to northern (Phitsanulok) and northeastern (Phetchabun [Kato & Koi 2009]) Thailand. *Hydrobryum phetchabunense* occurs in six streams in eastern Phitsanulok (Fig. 1). The population in Kaeng Lad waterfall is threatened by agricultural effluents, but other populations have maintained their size at other locations. *Hydrobryum phetchabunense* grows densely in Khlong Chompu stream. The extent of occurrence and area of occupancy are estimated at 3,634 km^2 and 4,190 m^2, respectively.

Conservation status. Near Threatened (NT).

Specimens examined. Northern Thailand, Phitsanulok Prov:, Nakhon Thai Dist., Phu Hin Rong Kla Natl. Park, Pha Lad waterfall, 1,180 m alt., 17°12'12.7″ N, 100°54'22.5″ E, 3 Dec. 2010, st. buds fl. fr., *PW & LA TWA-157*; 19 Dec. 2010, buds fl. fr., *PW & LA TWA-200*; 9 Dec. 2011, st. buds fl. fr., *PW & LA TWA-209*; 5 Dec. 2012, fl. fr., *PW & LA TWA-221*; Kaeng Lad waterfall, 312 m alt., 16°57'09.1″ N, 100°55'07.0″ E, 19 Dec. 2010, st. buds fl. fr., *PW & LA TWA-176*; 10 Dec. 2011, st. buds fl. fr., *PW & LA TWA-215*; 5 Dec. 2012, st. buds, *PW & LA TWA-226*; 23 Feb. 2015, fr., *MK et al. TL-1911*; Kaeng Khamuen, 225 m alt., 17°01'55.1″ N, 100°55'58.8″ E, 19 Dec. 2010, buds fl. fr., *PW & LA TWA-177*; 9 Dec. 2011, st. buds fl. fr., *PW & LA TWA-210*; 5 Dec. 2012, st. buds fl. fr., *PW & LA TWA-222*; Kaeng Sapung waterfall, 286 m alt., 16°56'43.1″ N, 100°54'21.2″ E, 29 Jan. 2011, buds fl. fr., *PW & LA TWA-202*; 7 Dec. 2012, st. buds fl. fr., *PW & LA TWA-233*; Kaeng Hin Sai waterfall, 261 m alt., 16°56'31.3″ N, 100°53'27.7″ E, 29 Jan. 2011, buds fl. fr., *PW & LA TWA-203*; 7 Dec. 2012, st. buds fl. fr., *PW & LA TWA-234*; Kaeng Pak Nao waterfall, 289 m alt., 16°56'54.6″ N, 100°54'19.1″ E, 7 Dec. 2012, st. buds fl. fr., *PW & LA TWA-235*. Nakhon Thai Dist.: Phu Kad Wildlife Sanctuary, Tadyai waterfall, 294 m alt., 17°15'0.1″ N, 100°53'53.1″ E, 6 Dec. 2012, st. buds fl. fr., *PW & LA TWA-230*; 19 Jan. 2013, fl. fr., *PW & LA TWA-255*; Huai Taleo waterfall, 475 m alt., 17°24'46.2″ N, 100°53'32.2″ E, 6 Dec. 2012, st., *PW & LA TWA-232*; 19 Jan. 2013, st. fl. fr., *PW & LA TWA-259*; Pha Tairuea waterfall, 185 m alt., 17°15'16.9″ N, 100°54'07.6″ E, 19 Jan. 2013, st., P*W & LA TWA-252*; Wanglum Bon waterfall 183 m alt., 17°15'07.2″ N, 100°54'04.0″ E, 19 Jan. 2013, st., *PW & LA TWA-253*; Wanglum Lang waterfall, 183 m alt., 17°15'06.2″ N, 100°54'03.0″ E, 19 Jan. 2013, st. fl. fr., *PW & LA TWA-254*. Noen Maprang Dist.: Tung Salaeng Luang Natl., Khlong Chompu stream, Kaeng Kanna, 81 m alt., 16°41'12.8″ N, 100°43'07.6″ E, 9 Feb. 2014, fl., fr., *PW & LA TWA-267*; 8 Apr. 2014, fr., *PW & LA TWA-291*; Kaeng Wang Kadum, 96 m alt., 16°40'37.3″ N, 100°43'32.1″ E, 10 Feb. 2014, fl., fr., *PW & LA TWA-274*; Kaeng Wang Tham Sang, 96 m alt., 16°40'47.0″ N, 100°43'36.8″ E, 10 Feb. 2014, fl., fr., *PW & LA TWA-277*; Kaeng Pak Klong Khunkrajiak, 97 m alt., 16°40'22.1″ N, 100°43'48.1″ E, 10 Feb. 2014, fl., fr., *PW & LA TWA-280*; Kaeng Wang Samnak, 104 m alt., 16°43'23.9″ N, 100°41'18.2″ E, 8 Apr. 2014, fr., *PW & LA TWA-293.*

Notes. Hydrobryum phetchabunense shows high phenotypic plasticity and is variable in the size of vegetative and reproductive structures and number of ovules per locule. Plants from Sai stream (*TWA-202, TWA-203, TWA-233, TWA-235*) and Khlong Chompu stream (*TWA-267, TWA-274, TWA-277, TWA-280, TWA-291, TWA-293*) are robust with all organs up to twice as long as those from other areas, including type locality, i.e., leaves 2–6 mm (*vs*. 1–3.5), flowering shoots 2–4 mm (*vs*. 1.5–2.5), bracts 0.5–2.5 mm (*vs*. 0.4–1.5), pedicels 0.5–2.5 mm (*vs*. 0.4–1.5), tepals 2.5–4 mm (*vs*. 1.5–3), stamens 3–8.5 mm (*vs*. 2–5), andropodium 1.5–5 mm (*vs*. 0.5–3), gynophores 0.5–3 mm (*vs*. 0.5–1.5), ovaries 1.5–2.5 mm (vs. 1–2), capsules 1.5–3 mm (*vs*. 1–2.5), capsule stalks 2–6 mm (*vs*. 1–2.5), and seeds 0.3–0.7 mm (*vs*. 0.3–0.5). Additionally, the plants from Khlong Chompu stream produce a vast range in number of ovules per locule, 8–23 (*vs*. 5–16). Compare with plants from the type locality in Phetchabun, the Phitsanulok plants have tightly arranged ovules (*vs*. loosely), more ovules per locule of 5–23 (*vs*. 4–8), and slightly fewer capsule ribs, (14–)16–18 (*vs*. 16–20). The number of capsule ribs is consistent in the Phitsanulok plants.

Phylogenetically *Hydrobryum phetchabunense* is divided into two clades, which are also geographically separated (P. Werukamkul & S. Koi unpubl. data). One comprises plants of Pran Ba waterfall, Nam Nao National Park in northeastern Phetchabun [*TL-1102* (type), *TKF-01*] and the other comprises those of eastern Phitsanulok (present study) and northwestern Phetchabun (L. Ampornpan & P. Werukamkul unpubl. data). The two clades differ in the number of ovules per locule and number of capsule ribs.

8. Hydrobryum tardhuangense M. Kato in Acta Phytotax. Geobot. 55(3): 148, f. 7. 2004; Koi & Kato in Kew Bull. 67(3): 349, f. 9. 2012; Werukamkul *et al.* in Acta Phytotax. Geobot. 63(1): 27. 2012.

Herbs, rheophilous, annual. Roots crustaceous, tightly attached to rock surface by adhesive hairs on lower surface, 0.1–0.7 (median, 0.2) mm thick, irregularly lobed, lobes 3–13 (5) mm wide; leaves tufted, scattered on dorsal surface of root, 2–11 (6) per tuft, surrounded by slightly raised rings of root tissue, 2–17 (7) mm long, linear, papillate, base sheath-like, apex obtuse. Flowering shoots on dorsal surface of root, appressed, 1.2–2.6 (2) mm long, 0.8–1.4 (1) mm wide; bracts papillate, 2–6 (4), in 2 rows, imbricate, 1–10 (1.5) mm long; base sheath-like, deltate, ovate, 0.5–1.5 (1) mm long, 0.5–1.5 (1) mm wide, margin reflexed, distal part acute, acuminate or caudate, 0.4–8.5 (0.5) mm long; spathella enclosing flower bud, papillate apically, minutely papillate in basally, ellipsoid, rupturing longitudinally at anthesis, persistent; flower 1, terminal; pedicel 0.3–1 (0.5) mm long; tepals 2, one on each side of andropodium, linear, 1.1–2.6 (2) mm long reaching about 2/3 of ovary, apex acute; stamens 2, 1.7–3.8 (3) mm long including anther, longer than pistil, forked 1/3–1/4 from apex, andropodium 1–2.6 (2.1) mm long, shorter or sometime as long as ovary; anthers basifixed, quadrangular, 0.2–0.5 (0.4) mm long, 0.3–0.5 (0.4) mm wide, dehiscing introrsely and longitudinally, pollen in dyads; gynophore 0.2–1 (0.6) mm long; ovary 1, light green, bilocular, ellipsoid, flattened, 1.2–2.1 (1.6) mm long, 0.8–1.1 (1) mm wide; stigmas bifid, forked near base, 0.3–0.7 (0.5) mm long, linear, papillate, pointed, curved, equal or subequal; ovules 10–32 (19) per locule on placental margin, or with 1–11 ovules in upper central area in addition to marginal ovules; capsule stalks 1–1.8 (1.3) mm long; capsules ellipsoid, flattened, 1.2-2.3 (1.8) mm long, 0.8–1.5 (1) mm wide, dehiscing by two equal valves, valves persistent, ribs 14-16 (16); seeds 14–42 (28) per capsule, oblong, obovoid or ellipsoid, 0.12–0.42 (0.25) mm long, 0.08–0.18 (0.12) mm wide.

Distribution. Northern (Phitsanulok) and northeastern [Loei (Kato 2004), Phetchabun (L. Ampornpan & P. Werukamkul unpubl. data)] Thailand and northern central Laos (Koi & Kato 2012). All distributional areas in Thailand are located in national parks. We found no reduction in population size. The extent of occurrence and area of occupancy in Thailand are estimated at 1,956 km^2 and 12,980 m^2, respectively.

Conservation status. Least Concern (LC).

Specimens examined. Northern Thailand, Phitsanulok Prov.: Nakhon Thai Dist., Phu Hin Rong Kla Natl. Park, Romklao Pharadon waterfall, 1,229 m alt., 16°59'12.1″ N, 100°59'41.0″ E, 3 Dec. 2010, st. buds fl. fr., *PW & LA TWA-155*; 19 Dec. 2010, buds fl. fr., *PW & LA TWA-201*; 5 Dec. 2012, st. buds *PW & LA TWA-223*; Water Turbine, 1,177 m alt., 16°59'11.8″ N, 100°59'38.8″ E, 3 Dec. 2010, buds fl. fr., *PW & LA TWA-156*; 19 Dec. 2010, buds fl. fr., *PW & LA TWA-199*; 24 Feb. 2015, fr., *MK et al. TL-1912*; 17 Jul. 2011, st. *PW & LA TWA-208*; 5 Dec. 2012, st. buds, *PW & LA TWA-224*.

Notes. The above description is applicable to plants in Phitsanulok. The Phitsanulok specimens differ from the Loei specimens (Kato 2004, Werukamkul *et al*. 2012) in the distal parts of the bracts varying from acute or acuminate to caudate (*vs*. acuminate, often caducous in individuals from Loei), and shorter andropodium, which is as long as the ovary or shorter (*vs*. much longer and extending beyond the pistil). Individuals from Phitsanulok are morphologically more similar to those from Laos (Koi & Kato 2012) than to the type specimen from Loei (Kato 2004). *Hydrobryum tardhuangense* is variable in the number of ovules per locule and the number of capsule ribs among the populations in Loei and Phitsanulok provinces and Laos (ovules 11-19, ribs 12–18 in Loei; ovules 10–32, ribs 14–16 in Phitsanulok; ovules 13–25, ribs 15–16 in Laos). A molecular phylogenetic analysis indicates that the plants (*TL-1912, TWA-199, TWA-201*) of Phitsanulok have the same *matK* sequence as the plants (*LK-113*) of Laos (Koi *et al*. 2012, S. Koi unpubl. data).

9. Thawatchaia trilobata M. Kato, Koi & Y. Kita in Acta Phytotax. Geobot. 55(2): 66, f. 1, 2, 3A-C. 2004; Kato in Acta Phytotax. Geobot. 55(3): 142, f. 4. 2004.

Distribution. Northern [Chiang Mai (Kato 2004) and Phitsanulok] and northeastern (Loei Province) Thailand. *Thawatchaia trilobata* in Loei (see Fig. 1 in Werukamkul *et al*. 2012) was not found from December 2009 to March 2012, but two of four subpopulations in Hueang River apparently have recovered (recent observation in April 2015). In Chiang Mai Province *Th. trilobata* occurs in several waterfalls in Mae Wang stream, Doi Inthanon National Park (Kato 2004). In Phitsanulok (Fig. 1) it forms dense mats on rock outcrops in a series of rapids in Khlong Chompu stream, Tung Salaeng Luang National Park. The extent of occurrence of the species in Thailand is estimated at 13,315 km^2.

Conservation status. Near Threatened (NT).

Specimens examined. Northern Thailand, Phitsanulok Prov.: Noen Maprang Dist., Tung Salaeng Luang Natl. Park, Khlong Chompu stream, Kaeng Kanna, 81 m alt., 16°41'12.8″ N, 100°43'07.6″ E, 9 Feb. 2014, fl. fr., *PW & LA TWA-268*; Kaeng Pak Kasao, 81 m alt., 16°41'11.2″ N, 100°43'22.7″ E, 9 Feb. 2014, st. fl. fr., *PW & LA TWA-271*; Kaeng Wang Kadum, 96 m alt., 16°40'37.3″ N, 100°43'32.1″ E, 10 Feb. 2014, fl. fr., *PW & LA TWA-275*; Kaeng Wang Tham Sang, 96 m alt., 16°40'47″ N, 100°43'36.8″ E, 10 Feb. 2014, fl. fr., *PW & LA TWA-278*; Kaeng Pak Klong Khunkrajiak, 97 m alt., 16°40'22.1″ N, 100°43'48.1″ E, 10 Feb. 2014, fl. fr., *PW & LA TWA-281*; Kaeng Taiwang-on, 77 m alt., 16°41'10.6″ N, 100°42'55.3″ E, 8 Apr. 2014, fr., *PW & LA TWA-295*; Kaeng Wang Takiannoi, 80 m alt., 16°41'07.9″ N, 100°42'44.8″ E, 8 Apr. 2014, fr., *PW & LA TWA-297*.

Notes. The number of ovules per locule are somewhat varies among populations; 7–9 in Chiang Mai (Kato 2004, Kato *et al*. 2004), 6–8 in Loei (Werukamkul *et al*. 2012), and 4–8 in Phitsanulok; but the number of ribs on the capsule is constantly 8–10.

Key to the species of Podostemaceae of Thailand

A key to the 42 species of Podostemaceae of Thailand was presented by Kato & Koi (2009). Because new species and new records were added, resulting in 49 species (Werukamkul *et al*.

Key to the species of Podostemaceae of Thailand

1a. Flowers 3-merous; perianth 3-lobed; stamens 2 or 3; ovary 3-locular; stigmas 3; leaves flattened, oblong or ovate, vein 1 (subfamily Tristichoideae) 2
1b. Flowers 2-merous; perianth with 2 filiform tepals; stamens 1 or 2; ovary 1- or 2-locular; stigmas 2; leaves filiform or vertically flattened, veinless (subfamily Podostemoideae) 15
2a. Roots subcylindrical or ribbon-like; shoots subcylindrical, simple or ramified; cupule absent, flower bud subtended by bracts 3
2b. Root absent; shoots crustose or rarely broadly ribbon-like, leafy on dorsal surface and at margin (not on ventral surface); flower bud covered by leafy cupule 11
3a. Reproductive shoot complex comprising 3 branches, middle vegetative, 2 laterals floriferous; leaves (=bracts) below flower many, in 6 rows, carinate .... ***Cussetia diversifolia***
3b. Reproductive shoot complex comprising 1–4 floriferous and 1–5 vegetative branches (ramuli), not arranged as above; flowering shoot bracts 2–several, thick or membranous 4
4a. Flowering shoots simple (with one terminal flower) or branched 5
4b. Flowering shoots simple, with one terminal flower, unbranched 6
5a. Shoots below flowers and ramuli ca. 1.5 mm thick; bracts several, phyllotaxis spiral or irregular; stamens 3 .... ***Terniopsis ramosa***
5b. Shoots below flowers and ramuli less than 1 mm thick; bracts 2, facing each other; stamens 2 .... ***Terniopsis chanthaburiensis***
6a. Vegetative shoots (ramuli) 3–90 mm long; number of stamens variable (2 and 3) 7
6b. Vegetative shoots (ramuli) 1.4–14 mm long; number of stamens nearly constant (2 or 3) 8
7a. Ramuli 10–90 mm long; pedicels 7–15 mm long; stamens 5–6 mm long; ovules 8–12 per locule .... ***Terniopsis ubonensis***
7b. Ramuli 3–20 mm long; pedicels 2–4 mm long; stamens 2–4 mm long; ovules 25–35 per locule .... ***Terniopsis malayana***
8a. Stamens 3, rarely 2; stigmas cristate when young, forked and filiform at maturity .... ***Terniopsis filiformis***
8b. Stamens 2, rarely 3; stigmas cristate 9
9a. Vegetative shoots (ramuli) simple; flower associated with single ramulus .... ***Terniopsis brevis***
9b. Vegetative shoots (ramuli) branched; flower associated with 1–4 ramuli 10
10a. Ramuli 1- or 2- (or 3-)branched near base, 1.4–14 mm long .... ***Terniopsis heterostaminata***
10b. Ramuli 1–4, branched near base, 2–7 mm long .... ***Terniopsis minor****
11a. Shoots 3–20 mm wide or wider; dorsal leaves arranged in branched longitudinal rows; pedicels 3–10 mm long 12
11b. Shoots 1–2.5 mm wide; dorsal leaves in 1–2 inconspicuous rows; pedicels 1.5–7 mm long 14
12a. Leaves of rosette to 6.2 mm long, leaves on cupule variably distributed, sparse or caducous in middle zone, to 4 mm long .... ***Dalzellia sparsa****
12b. Leaves of rosette to 3 mm long, leaves on cupule evenly distributed, to 1 mm long 13
13a. Dorsal leaves dense, fimbriate; marginal leaves narrowly deltate, to 1.5 mm long; leaves on cupule 0.5–1 mm long; ovules ca. 30 per locule .... ***Dalzellia ubonensis***
13b. Dorsal leaves sparse, separate; marginal leaves deltate-lanceolate, to 2 mm long; leaves on cupule 0.3–0.4 mm long; ovules 50–60 per locule .... ***Dalzellia ranongensis***
14a. Shoots 1.5–2.5 mm wide; pedicels 1.5–2 mm long, as long as ovary; ovules 50–60 per locule .... ***Dalzellia kailarsenii***
14b. Shoots 1–1.5 mm wide; pedicels 2–7 mm long, longer than ovary (1.3–1.5 mm); ovules 30–50 per locule .... ***Dalzellia angustissima***
15a. Roots subcylindrical or ribbon-like 16
15b. Roots crustose 33
16a. Bracts 3- or 4-lobed or digitate; capsules globose, smooth (or weakly striped), or ellipsoid, ribbed 17
16b. Bracts simple; capsules ellipsoid, slightly flattened, 8–15-ribbed 20
17a. Holdfasts present on ventral surface of root under tufts of leaves; tufts of leaves and flowering shoots borne on flank of root between successive root branches and at sinuses of root branches 18
17b. Holdfast absent; tufts of leaves and flowering shoots only at sinuses of root branches 19

18a. Bracts linear-oblong, with 2 small lateral basal lobes; capsules globose, smooth .... ***Paracladopus chiangmaiensis***
18b. Bracts digitate; capsules ellipsoid, 12–14-ribbed .... ***Paracladopus chanthaburiensis***
19a. Bracts 3- or 4-lobed, lobes semicircular, thin, smooth .... ***Cladopus taiensis***
19b. Bracts digitate, segments finger-like, thick, papillate with silica .... ***Cladopus fallax***
20a. Stamens 2; capsule ribs 8 21
20b. Stamen 1; capsule ribs 8–15 23
21a. Tufts of leaves and flowering shoots at sinuses between root branches; bracts ovate or ovate-lanceolate, apical portion linear, caducous; capsule-valves unequal .... ***Zeylanidium lichenoides***
21b. Tufts of leaves and flowering shoots on flanks of root between successive root branches; bracts lanceolate or ovate-lanceolate, apex obtuse or sometimes acute; capsule-valves equal .... ***Polypleurum wallichii*** (22)
22a. Roots ca. 5 mm wide; leaves to 5(–10) mm long; pedicels 5–8 mm long; ovaries to 2.5 mm long .... ***var. wallichii***
22b. Roots ca. 3 mm wide; leaves to 2.5 mm long; pedicels to 2–4 mm long; ovaries 1.2–1.5 mm long .... ***var. parvum***
23a. Tufts of leaves borne on flank of root between successive root branches; capsule ribs 8–12 24
23b. Tufts of leaves or shoots borne exclusively at sinuses of root branches; capsule ribs 10–15 25
24a. Roots 2–4 mm wide; pedicels 6–7 mm long; ovaries protruding from spathella at anthesis, 2-locular; stigmas much shorter than ovary; capsule ribs 8 .... ***Polypleurum schmidtianum***
24b. Roots 1–1.5 mm wide; pedicels to 1 mm long; ovaries mostly enclosed in spathella at anthesis, 1-locular; style plus stigmas as long as ovary or longer; capsule ribs 10–12, inconspicuous .... ***Polypleurum longistylosum***
25a. Shoots prominent, elongate; leaves exposed on stems; flowers always or occasionally multiple per shoot ... 26
25b. Shoots comprising tufts of leaves, lacking stems; leaf-bases embedded within root; flowers exclusively 1 per shoot 27
26a. Roots 1–1.5 mm wide; shoots to 5 cm long, simple, erect; leaves 15–30 mm long .... ***Polypleurum erectum***
26b. Roots 2.5–4 mm wide; shoots to 1 m long, branched, bent at base and floating; leaves 30–70 mm long .... ***Polypleurum longicaule***
27a. Bracts 4–6; pedicels 10–15 mm long; spathellas 4–6 mm long .... ***Polypleurum phuwuaense***
27b. Bracts 2–4(–6); pedicels 2–8 mm long; spathellas 2–4 mm long 28
28a. Stamens 1–1.2 mm long 29
28b. Stamens 1.5–3.9 mm long 31
29a. Leaves 20–40 mm long; stigmas subdeltoid or deltoid-ovate .... ***Polypleurum longifolium***
29b. Leaves 5–15(–45) mm long; stigmas linear, narrowed to apex (leaves 4.5–45 mm long, stigmas linear or subulate in *P. pluricostatum*) 30
30a. Roots 1.5–3 mm wide; stalk of capsule 5–8 mm long; ovules ca. 30 per locule ... ***Polypleurum wongprasertii***
30b. Roots 1–2 mm wide; stalk of capsule 2.5–4 mm long; ovules 10–20 per locule .... ***Polypleurum insulare***
31a. Stigmas semicircular; ovules 40–70 per locule .... ***Polypleurum sisaketense***
31b. Stigmas narrowly conical, subdeltoid or deltoid-ovate; ovules 10–30 per locule (14–60 in *P. pluricostatum*) 32
32a. Bracts 2–4; pedicels 4–8 mm long; stamens 1.5–2 mm long; stalk of capsule 5–9 mm long .... ***Polypleurum prachinburiense***
32b. Bracts 2(–4); pedicels 2.5–5 mm long; stamens 1.5–3.9 mm long; stalk of capsule 2.6–6 mm long .... ***Polypleurum pluricostatum***
33a. Flowering shoots usually erect; bracts in 4 rows, dimorphic, ventral (facing root) bilobed, dorsal entire 34
33b. Flowering shoots usually appressed or oblique or only flowers erect; bracts in 2 rows, uniform, entire or trilobed 35
34a. Tepals 2.2–4.5 mm long; capsules 1.1–2.5 mm long, ribs 8–16 including short thin ribs .... ***Hanseniella heterophylla****
34b. Tepals to 1.5 mm long; capsules 1-2 mm long, ribs 8 .... ***Hanseniella smitinandii***
35a. Bracts trilobed; apex of spathellas mucronate .... ***Thawatchaia trilobata****
35b. Bracts entire; apex of spathellas without mucro 36
36a. Stamens 2; filament forked 37
36b. Stamen 1, filament simple 48
37a. Apex of bracts obtuse or truncate 38
37b. Apex of bracts acute, acuminate or caudate 44
38a. Stigmas broad, cristate, apex truncate or emarginate 39
38b. Stigmas narrow, linear, ligulate, apex pointed or obtuse 40
39a. Stigmas cristate .... ***Hydrobryum griffithii***
39b. Stigmas truncate or emarginate .... ***Hydrobryum chiangmaiense***

40a. Ovaries 1-locular .... ***Hydrobryum somranii***
40b. Ovaries 2-locular 41
41a. Ovules on marginal surface of placenta 42
41b. Ovules on marginal or whole surface of placenta except on small lower central area 43
42a. Ovules (8–)11–16 per locule; capsule ribs 10–14 .... ***Hydrobryum japonicum***
42b. Ovules large 4–11 per locule; capsule ribs 16–20 .... ***Hydrobryum loeicum***
43a. Tufts of leaves surrounded by slightly raised fringe of root tissue; ovules 5–23 per locule; stalk of capsule 1–6 mm long .... ***Hydrobryum phetchabunense****
43b. Tufts of leaves not surrounded by raised ring of root (root even around tufts of leaves); ovules 8–28 per locule; stalk of capsule 1–2 mm long .... ***Hydrobryum vientianense***
44a. Spathellas rupturing apically; stigmas markedly unequal 45
44b. Spathellas rupturing longitudinally; stigmas equal or subequal 46
45a. Tufts of leaves surrounded by prominently raised ring of root; bracts 2–12, 2–5(–8) mm long, apex acuminate 1–4 mm long .... ***Hydrobryum kaengsophense****
45b. Tufts of leaves surrounded by less markedly raised ring of root; bracts 2–4, 3.5–10.5 mm long, apex acuminate 2–9 mm long .... ***Hydrobryum bifoliatum****
46a. Bracts to 13 mm long, base semicircular, apex caudate .... ***Hydrobryum phurueanum***
46b. Bracts to 10 mm long, base deltate, apex acute, acuminate, or caudate 47
47a. Bracts 1–4.5 mm long; pedicels 0.6–2 mm long; gynophores 0.5–1.6 mm long; capsule ribs 12–14, stalks 1.5–3 mm long .... ***Hydrobryum varium***
47b. Bracts 1–10 mm long; pedicels 0.3–1 mm long; gynophores 0.2–1 mm long; capsule ribs 12–18, stalks 0.7–1.8 mm long .... ***Hydrobryum tardhuangense****
48a. Ovaries 2-locular 49
48b. Ovaries 1-locular .... ***Hydrobryum micrantherum*** (50)
49a. Bracts ovate, apex obtuse but basal ones sometimes needle-like; anthers dehiscing longitudinally; ovules on marginal surface of placenta .... ***Hydrobryum khaoyaiense***
49b. Bracts deltate, apex acute, acuminate or caudate; anthers dehiscing tortuously; ovules on mostly whole surface of placenta .... ***Hydrobryum mandaengense****
50a. Roots (crusts) 0.1–0.2 mm thick; bracts 2–4; ovaries ca. 1.5 mm long; ovules 9–13 per each side of placenta .... **var. *micrantherum***
50b. Roots (crusts) 0.2–0.3 mm thick; bracts 3–5; ovaries 1.5–2 mm long; ovules 13–23 per each side of placenta .... **var. *crassum***

*species from Phitsanulok.

2012, present study), the key is updated here. Asterisks indicate species from Phitsanulok.

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